Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*

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Summary

1. Anthropogenic noise is rapidly increasing in wilderness areas as a result of industrial expansion. While many road studies have attempted to assess the effects of industrial noise on birds, conflicting factors such as edge effects often inhibit the ability to draw strong conclusions.

2. We assessed pairing success and age distribution of male ovenbirds *Seiurus aurocapilla* in the boreal forest of Alberta, Canada, in areas around noise-generating compressor stations compared with areas around habitat-disturbed, but noiseless, wellpads. This allowed us to control for edge effects, human visitation and other factors that are not controlled for in studies of noise generated by roads. Generalized estimating equations (GEE) were used to assess the impacts of noise on ovenbird pairing success, age structure and body morphology.

3. We found a significant reduction in ovenbird pairing success at compressor sites (77%) compared with noiseless wellpads (92%). These differences were apparent regardless of territory quality or individual male quality. Significantly more inexperienced birds breeding for the first time were found near noise-generating compressor stations than noiseless wellpads (48% vs. 30%).

4. While there are multiple proximate explanations for these results, the ultimate cause of the changes seems to be noise pollution. We hypothesize that noise interferes with a male's song, such that females may not hear the male's song at greater distances and/or females may perceive males to be of lower quality because of distortion of song characteristics.

5. *Synthesis and applications.* This work demonstrates that chronic background noise could be an important factor affecting bird populations. It can impact upon pairing success and age structure of passerines; in boreal Alberta this could pose a problem for certain species as energy development expands rapidly.

Key-words: age structure, compressor stations, industrial impacts, noise, ovenbird, pairing success

Introduction

Many factors contribute to the ability of male birds to attract a female during the breeding season. Individual 'quality' is usually measured by age, size or body condition; these attributes and how they influence song quality are often identified as key determinants of the attractiveness of males to females (Breitwisch 1989; Holmes, Marra & Sherry 1996). High-quality individuals are often found in habitats where nesting success and number of young fledged are highest (Holmes, Marra & Sherry 1996). Physical changes to habitat caused by human activity can reduce the quality of habitat for many birds by decreasing nest success, reducing food supply and decreasing survival. These effects may interact to create a situation whereby lower-quality males settle in disturbed habitats and as such are less likely to attract a mate because of female avoidance of disturbed habitats and/or the 'lower quality' of males that settle there (Villard, Martin & Drummond 1993; Reijnen & Foppen 1994; Van Horn, Gentry & Faaborg 1995; Lambert & Hannon 2000; Bayne & Hobson 2001). While most research on how avian pairing success is affected by anthropogenic impacts deals with physical factors such

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as edge and landscape condition, it is possible that non-physical anthropogenic impacts may also diminish the ability of male birds to attract females. As birds communicate primarily by sound, loud ambient noise caused by human activities could inhibit communication between conspecifics, potentially reducing pairing success. Birds in forests typically have songs characterized by low frequencies (*c.* 1·5–4·0 kHz). These frequencies seem to provide optimal long-distance song transmission range in complex forest structures (Brenowitz 1982; Slabbekoorn, Ellers & Smith 2002). As a result, much bird song lies in the same part of the frequency spectrum occupied by many types of mechanical noise (Binek 1996; ATCO Noise Management 2003). Because of this overlap, industrial noise may interfere with bird communication occurring via song. If the ability to communicate with females is influenced by anthropogenic noise, then we might expect males in high noise areas to be less likely to attract a mate.

The limited research on the effects of chronic anthropogenic noise and birds has indirectly examined the effects of traffic noise on bird populations near highways. Many species of bird have been found to exhibit reduced breeding densities in areas around roads, with noise assumed to play a larger role in that reduction than either visibility of cars or traffic mortality (Reijnen *et al*. 1995; Kuitunen, Rossi & Stenroos 1998). A few studies have also shown that birds have reduced breeding success (i.e. a lower probability of mating or successfully rearing young) near roads (Reijnen & Foppen 1994; Burke & Nol 2000; Kuitunen *et al*. 2003). However, it has never been demonstrated conclusively that the noise generated by roads is the factor that results in reduced breeding activity in birds; the myriad of other potential impacts of roads (e.g. edge effects and traffic-caused mortality) have not been effectively controlled for.

Boreal Alberta is one of North America's most intense oil and natural gas production areas. Throughout the region, a network of pipeline systems connects gathering sites to processing facilities and ultimately transport terminals. Along these pipeline systems lie compressor stations, which function to boost pressure in the pipelines and help maintain the flow of natural gas and oil from wells. A typical compressor station consists of one to three motors cooled by an equal number of large fan units; the machinery is housed in an aluminium shed in a 1- to 2-ha cleared area in the forest. These motors and fans run continuously other than for infrequent maintenance, and typically produce chronic noise levels of 75–90 dB(A) near the source (Bolstad Engineering Associates 1978; ATCO Noise Management 2003) but can reach 105 dB(A) (MacDonald, Ewanek & Tilley 1996). Under 'free field' conditions, noise is reduced by 6 dB(A) for every doubling of distance from the source (ATCO Noise Management 2003); this loss is accelerated in forested systems, dependent on the type of forest and understorey structure (Huisman & Attenborough 1991). However, low-frequency mechanical noise can be transmitted far from the source despite this reduc-

tion in amplitude (Bolstad Engineering Associates 1978; Brenowitz 1982).

The range of noise intensity produced by compressor stations is similar to those in studies that have found negative effects on birds as a result of purported 'road noise'. At compressor stations, however, many of the confounding variables associated with roads are absent or can be more effectively controlled for. Vehicle traffic to compressor stations in forests is typically minimal, having only a few vehicles visiting per day. Compressor stations in forest environments are associated with a significant amount of edge habitat, as are roads. This correlation between noise and edge makes it difficult to separate the impacts on birds of noise relative to edge. Simply comparing bird responses at distances away from compressor stations confounds noise effects with edge effects, an issue that has not been well addressed by road noise studies. However, associated with pipelines are wellpads. Like compressor stations, wellpads are clearings of 1- to 2-ha of forest habitat that are linked via narrow linear features such as pipelines and single-lane road access. However, wellpads, unlike compressor stations, produce no chronic noise and thus provide an effective control for separating the effects of edge relative to noise.

The objective of this study was to test whether noise decreases habitat quality in the breeding range for the neotropical migrant ovenbird *Seiurus aurocapilla* (Linnaeus 1766) by examining pairing success close to compressor stations relative to wellpads. By capturing birds and obtaining information on individual attributes we were also able to examine some of the proximate mechanisms that influence the ability of a male bird to attract a female in noisy vs. quiet environments. The ovenbird was selected as the study species because of a male-dominated sex bias in most populations, its apparent sensitivity to habitat disturbance caused by anthropogenic activity, the fact that it is a ground-dweller, making it relatively easy to capture and track, and its high density in the western boreal forest (Villard, Martin & Drummond 1993; Van Horn, Gentry & Faaborg 1995; Lambert & Hannon 2000; Bayne & Hobson 2001). In addition, the ovenbird has an inflexible song relative to other species (Lein 1981), suggesting little ability of males to adapt their song to be heard above anthropogenic noise. Ovenbird song frequency (with a minimum frequency of *c.* 2 kHz) also overlaps with that of compressor station noise.

Methods

STUDY AREA

Our research was conducted in two regions of northern Alberta, Canada, between 54° and 59° latitude and 110° and 119° longitude. The region has significant energy sector development, with roads, industrial sites and seismic lines being the prominent form of human disturbance. The study area contains *c.* 900 compressor stations in an approximately 10-million ha area.
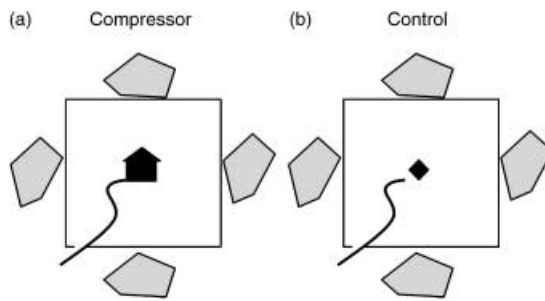
Fig. 1. Study design for ovenbird capture in northern Alberta, Canada, in 2004 and 2005. One ovenbird was captured on each side of an energy industry-created clearing (territories indicated by grey polygons). Compressor sites had a noise-generating compressor station (house icon) at the centre of the clearing, while control sites had a noiseless wellhead (diamond icon) at the centre.

Forests in the region consist of boreal mixed wood and peatland vegetation (Strong & Leggat 1992). Lowland vegetation is dominated by black spruce *Picea mariana* (Mill.), bogs and fens, while upland areas are dominated by trembling aspen *Populus tremuloides* (Michx.) and white spruce *Picea glauca* (Moench).

SITE SELECTION

Birds were observed at two types of sites, compressor stations and wellpads (hereafter compressor sites and control sites). All sites were rectangular clearings in the forest that had been created for energy industry operations. Clearings measured *c.* 200–400 m side^{-1}. Compressor sites had a compressor station with one to three fan units at the centre of the cleared pad. Control sites were pads of a similar size. Most of these had wellheads at the centre, although some had meter stations or other small facilities that produced no noise. While some wells and meter stations occasionally produced a very quiet and periodic hissing sound, the only chronic noise at control sites was wind-generated. Both types of site had similar physical disturbances such as pipelines and road access (Fig. 1).

Site selection was carried out using ArcGIS 9·0 (ESRI Inc., Redlands, CA) using Alberta Vegetation Inventory (AVI) data, energy facility data and road data obtained from Alberta Pacific Forest Industries (Boyle, Canada), Tolko Forest Industries (High Level, Canada) and Daishowa-Marubeni International Ltd (Peace River, Canada). Our research was conducted entirely in mature, 60–90-year-old aspen forest (the primary habitat of breeding ovenbirds) to reduce the effects of vegetation structure as a factor influencing habitat quality for birds. All sites selected in the GIS were ground-truthed to ensure that the energy facility was appropriate and vegetation type was accurate. Within the pool of sites having appropriate forest cover, site selection was constrained by the following criteria: all selected sites were truck-accessible, and sites were close enough together to make travel between sites practical on a daily basis. Compressor sites were

> 3 km away from other sites to ensure that no noise contamination from one site would reach another. Control sites were occasionally < 3 km away from each other for logistical reasons; however, as no noise was emitted from these sites noise contamination was not a concern. While forestry is a major industry in the study areas, no study sites were located within 1 km of existing clearcuts or within 2 km of ongoing forestry operations at the time of the study.

OVENBIRD CAPTURE

Male ovenbirds were captured in the spring of 2004 and 2005. We captured birds in approximately equal numbers at compressor sites and control sites (hereafter compressor and control birds, respectively). All captures were conducted between 24 May and 22 June, with the majority of birds captured before 9 June. Birds captured after that date were usually replacements that had assumed the territory of birds that had been ringed but who had vacated the area post-capture. These 'missing' birds were presumed not to have permanently settled in the territory and were excluded from all analyses. Capture attempts were focused on the early morning (04:00–10:00) but during the peak capture period birds were caught at all times of day.

To locate birds on which to evaluate pairing status, we walked the perimeter of the cleared pad listening for male ovenbirds singing near the forest's edge. If an ovenbird was heard, and estimated to be < 200 m from the clearing edge, we targeted it for capture. If during a walk of the perimeter no ovenbirds were heard, we would repeat the walk while playing recordings of male ovenbird songs from speakers. It is possible that locating birds by playback resulted in birds moving closer to the edge than they would have been found otherwise; however, it is reasonable to assume that ovenbirds responding to the playback of a rival male's song would remain within the boundary of their territories. Therefore, all birds caught were likely to be the closest inhabitants to the edge.

We used mist-nets together with male ovenbird song playback to draw birds into the net. Once captured, birds were sexed based on the presence of a cloacal protuberance (Pyle *et al.* 1987); female birds were released. Each male bird received a Canadian Wildlife Service (Ottawa, Canada) aluminium ring and three coloured-plastic leg rings to form a unique ring combination. We measured unflattened right wing chord (mm), tail length (mm), right tarsal length (mm) and mass (g) of each bird (Pyle *et al.* 1987). We derived a condition index by dividing mass by wing chord (Burke & Nol 2001). We also plucked the third right rectrix in order to age the bird. Following the capture procedure, the bird was released; pairing observations did not commence until at least the next day.

PAIRING OBSERVATIONS

Each ringed ovenbird was identified based on its colour bands, and followed to determine whether or not it

was able to pair successfully with a female. Our pairing success protocol followed those of Lambert & Hannon (2000) and Bayne & Hobson (2001). Birds were followed for up to 90 min over the breeding season or until a sign of pairing was observed. Signs of pairing included observing: (i) the male in the vicinity of a female; (ii) the male carrying food; (iii) the male or female with nesting material; (iv) the male or female with young; or (v) an active nest within the male's territory (Bayne & Hobson 2001). As ovenbirds are monomorphic, a non-singing individual tolerated by a male within a 5-m radius or emitting a series of 'tsip' notes was considered its female mate, as females often make those vocalizations in response to their mate's song (Lein 1980).

Birds were tracked for a maximum of 30 min^{-1} day, with track time being accumulated when the bird was in sight or in continuous song within 30 m of the observer. Tracking days were spread out over the breeding season; all efforts were made to have a minimum of one 30-min tracking period during the prime courting and nest-building period (*c.* 27 May–9 June). For birds who were not determined to be paired before *c.* 9 June, a second tracking period was attempted during the female's nesting period when the male is feeding the young (until *c.* 19 June), and a third after the chicks had left the nest (beginning *c.* 20 June), ensuring that birds that may have acquired mates late in the season had adequate track time.

OVENBIRD AGEING

By measuring the tip angle of the third right rectrix, it is possible to classify an ovenbird as either a second-year (SY) bird or an after-second-year (ASY) bird (Donovan & Stanley 1995). SY birds are inexperienced breeders breeding for the first time (hereafter young birds), while ASY birds had potentially bred the year before (hereafter old birds). Ageing birds in this manner is possible because ovenbirds retain their juvenile tail feathers through their first winter season and do not moult them until after their first breeding season (Pyle *et al.* 1987). These feathers are often tapered, compared with the paddle shape of post-moult rectrices present in ASY individuals (Pyle *et al.* 1987). Feathers were scanned into a computer and images expanded by a constant size. Images were printed in greyscale and the angle of the feather tip calculated using transparent grid paper and a small ruler. Birds having a rectrix tip angle of < 84° were classified as SY; those having tip angles > 84° were classified as ASY (Bayne & Hobson 2001). With this criterion we were able to age all individuals, albeit with some uncertainty. Donovan & Stanley (1995) demonstrated that birds with tip angles > 90° were ASY and < 78° were SY with 99% certainty. During analysis, we used both criteria for ageing. Feathers were classified blindly by bird identification number without knowledge of which treatment group that individual belonged to.

TERRITORY VEGETATION MEASUREMENTS

We conducted a vegetation survey in the estimated territory of each ringed male ovenbird via four 1-m wide, 25-m long transects orientated along a random bearing. Transects were spaced 10 m apart and were based around the centre of the territory, as defined by the cumulative observations of that bird's behaviour. We measured diameter at breast height (d.b.h.) of all trees that intercepted the transect. We used a 'bird-centric' definition of tree. Any vegetation > 5 m in height was classified as a tree, and all stems emerging from the same individual plant were measured separately. While walking transects, we recorded the number of downed woody material (DWM) pieces > 8 cm in diameter that the transect intercepted.

Along each transect, five 0·25-m^2 plots were placed at 5-m intervals. In each plot, we measured shrub species, density (number of stems of each species) and height category (0·5–2 m or > 2 m). We also measured the leaf litter depth at the centre of each plot with a metal metre stick, and estimated percentage cover of forbs, moss and grass in each plot based on five categories (0, none present; 1, 1–25% cover; 2, 26–50% cover; 3, 51–75% cover; 4, 76–100% cover). For analysis, all vegetation measurements were averaged for each ovenbird's territory. Shrub density was transformed into two variables, density of short shrubs and density of tall shrubs. Tree data were summarized into density of hardwood and softwood trees.

STATISTICAL ANALYSIS

To evaluate whether ovenbirds at compressor sites had lower pairing success than at control sites, we used a generalized estimating equation (GEE) with a binomial error structure and a logit link within STATA 9·1 (STATA Corp., College Station, TX). GEE are a modification of generalized linear models that account for the nested structure in an experimental design, whereby each individual occurs at a site with the site being the primary sampling unit (Hardin & Hilbe 2003). Within the GEE framework, the pairing status of the multiple birds sampled at each site is assumed to be correlated to an extent that is estimated by the model. By estimating the exchangeable correlation in pairing status of individuals within the same site, estimates of standard errors are robust to any lack of independence. A priori we predicted that noise would reduce pairing success, so our tests for noise effects were all one-tailed.

This study was designed to minimize any variation in habitat quality as a result of vegetation structure. However, variation in habitat quality for attributes that were not effectively described by AVI data could have been a confounding factor in our design. To control for any vegetation effects, we used principal components analysis (PCA) in STATA 9·1 to summarize the variation in vegetation structure for all territories. All vegetation variables were standardized to zero mean and unit

Table 1. Summary of male ovenbirds captured and ringed per treatment per year, and the number of birds on which pairing observations were made. Compressor sites (*n* = 20) had a noise-generating compressor station at the centre of a forest clearing, while control sites (*n* = 21) had a noiseless wellhead at the centre. The study was conducted in northern Alberta, Canada, in 2004 and 2005

	2004		2005		Total number of birds used
	Captured	Missing	Captured	Missing	
Control	47	8	26	7	58
Compressor	44	7	31	13	55
Total	91	15	57	20	113

variance prior to PCA. PCA of DWM, forb cover, moss cover, grass cover, litter depth, high shrub density, low shrub density, hardwood tree density and softwood tree density resulted in two principal component axes that together explained 40% of the variation in the original data set. The first factor represented territories with large trees, higher shrub density and more DWM (positive loading on component 1, hereafter territory structure). The second factor represented territories that varied in the proportion of deciduous to conifer trees (positive loading for deciduous tree density, hereafter territory composition). Territory structure and territory composition were included in the GEE model to ensure that any confounding effects of vegetation as a measure of territory quality were controlled for when assessing the effects of noise. As vegetation factors were simply nuisance variables with no a priori predictions regarding direction, we report their statistical significance as two-tailed tests.

Male quality as measured by age and body morphology has been shown to be an important determinant of pairing success in other studies (Saether 1990; Bayne & Hobson 2001). If there is no effect of noise on ovenbirds, then a priori we predicted that there should be no differences in age structure or body morphology of birds between compressor and control sites. However, if noise does affect pairing success it may do so by influencing the quality of the individuals that settle at compressor vs. control sites. A GEE was used to test whether the frequency of occurrence of old vs. young birds differed between these sites. We tested this hypothesis using both the 84° tip angle criterion and the more stringent 78°/90° rule. We also tested whether bigger birds or those in better condition were less likely to settle at compressor vs. control sites. GEE were used to analyse these data with respect to noise treatment. In this analysis we assumed a Gaussian error structure and identity link. Vegetation structure within territories was controlled for in all analyses. A priori we predicted that larger and older birds in better condition would be more likely to settle at controls than at compressors so these statistical tests are one-tailed.

All results are reported as odds-ratios (OR) or slope coefficients (α). Statistical tests are reported as *z*-scores from GEE unless otherwise stated, with probability values derived as discussed above. All tests were considered significant at *P* = 0.05.

Table 2. Contingency table illustrating ovenbird pairing success and age distribution between treatments. SY birds are first-year breeders, while ASY birds are in at least their second breeding season. Compressor sites had a noise-generating compressor station at the centre of a forest clearing, while control sites had a noiseless wellhead at the centre. The study was conducted in northern Alberta, Canada, in 2004 and 2005

Treatment Status	Compressor		Control		Total
	Paired	Unpaired	Paired	Unpaired	
Age					
SY	20	6	17	0	43
ASY	23	4	34	4	65
Unaged	1	0	1	0	2
Total	44	10	52	4	110

Results

PAIRING SUCCESS

A total of 148 birds was captured over the 2004 and 2005 breeding seasons at 20 compressor sites and 19 control sites. Data were pooled across years for all analyses. Summary data are presented in Table 1. All birds that had gone missing and were not relocated (*n* = 35) were excluded from all analyses. A contingency table analysis with a chi-square test demonstrated no significant difference in the number of birds that went missing between the two treatments ($\chi^2 = 0.77$, d.f. = 1, *P* = 0.38). There was also no difference in the number of birds that went missing between age categories ($\chi^2 = 1.76$, d.f. = 1, *P* = 0.18). We were unable to amass 90 min of pairing observations, or observe a conclusive pairing sign, on three birds (two control birds and one compressor bird). These birds were also excluded from analyses.

For the remaining 110 birds we identified 92% of control birds as paired compared with 77% of compressor birds (Table 2). Controlling for territory structure and composition, we found that pairing success was significantly lower for compressor birds than control birds (OR = 0.31, *z* = −2.11, *P* = 0.02). Territory structure was also a significant predictor of pairing success (OR = 1.49, *z* = 2.2, *P* = 0.03), while territory composition was not (OR = 0.87, *z* = −0.63, *P* = 0.53). The within-site correlation estimated by the GEE was *r* = −0.12.

OVENBIRD AGE

Again, all birds that were categorized as missing were excluded from analyses. Among the remaining birds ($n = 111$), 70% of birds at control sites ($n = 57$) were classified as ASY compared with 52% at compressor sites ($n = 54$), using the 84° rule. If we discounted all birds whose tip angles were between 78° and 90° ($n = 31$), 79% of birds at control sites were classified as ASY ($n = 33$) compared with 53% at compressor sites ($n = 20$), an even greater difference. Because of this, we chose the more conservative 84° rule for further analyses. For birds whose pairing status was determined ($n = 108$), there was a significant difference in age structure between treatments (OR = 0·50, $z = -1·68$, d.f. = 1, $P = 0·046$). Age was not a significant determinant of pairing success, however (OR = 1·26, d.f. = 1, $z = 0·41$, $P = 0·69$). The discrepancy in sample size was because of two birds from which tail feathers were not collected so ageing was not possible. The within-site correlation for age structure was very low at $r = 0·001$.

BODY MORPHOLOGY

Estimates of wing, tail and mass were available for 107 individuals for whom pairing success was determined. There was no relationship between bird age and tail length ($\alpha = 0·94$, $z = 1·44$, d.f. = 1, $P = 0·07$), mass ($\alpha = 0·12$, $z = 0·55$, d.f. = 1, $P = 0·29$) or body condition ($\alpha = 0·01$, $z = 0·95$, d.f. = 1, $P = 0·17$), although wing chord was significantly longer in older birds ($\alpha = 1·09$, $z = 2·48$, d.f. = 1, $P = 0·007$). After controlling for age, there was no significant difference in any of the four body variables between compressor and control sites (all $P > 0·05$).

INDIVIDUAL QUALITY VS. HABITAT QUALITY

A model containing habitat structure, habitat composition, noise status, individual age and individual morphology was created to determine the relative importance of individual quality vs. habitat quality as factors influencing pairing success. In this model, the only two variables that were statistically significant were noise status (OR = 0·30, $z = -2·1$, d.f. = 1, $P = 0·02$) and territory structure (OR = 2·1, $z = 2·3$, d.f. = 1, $P = 0·02$).

Discussion

PAIRING SUCCESS

Competition to attract females seems to be intense for male ovenbirds across their range, as almost all studies have found pairing success to be < 100% (Villard, Martin & Drummond 1993; Van Horn, Gentry & Faaborg 1995; Lambert & Hannon 2000; Bayne & Hobson 2001). This indicates that a biased sex ratio exists in ovenbird populations, which seems to result in strong selection by females for high-quality males or

males having high-quality territories. Our results suggest that females are selecting high-quality (i.e. quiet) territories rather than older or bigger males. Admittedly, however, the small sample size of unpaired males makes age and body morphology effects difficult to detect. Noise level from industrial activity seems to be one habitat factor that females use when deciding how to choose a mate, as we found a 15% difference in pairing success between ovenbirds at sites having industrial background noise and those without.

A probable explanation for the reduction in likelihood of male–female mating encounters is that intersex ovenbird communication is being reduced by chronic background noise. If noise interferes with a male's song it may not be audible to females over as great a distance, thereby reducing the pool of females who may potentially respond to his song. Alternatively, females may perceive males as being of lower quality than they actually are because of distortion of song characteristics. Ovenbirds have a high-amplitude song relative to most wood warblers in North America yet they still exhibit a reduction in pairing success, suggesting that other species with quieter songs may be similarly affected. Alternatively, other forms of communication may be impacted by industrial noise. Predator detection may be inhibited, resulting in increased mortality of females. This risk may be particularly high for female ovenbirds as they nest on the ground and are the sole incubators. Male and female ovenbirds have a considerable repertoire of quiet call notes (Lein 1980) that they use when directly communicating with their mate (e.g. signalling when the female leaves the nest) that also may be more difficult to hear in noisy environments. While nesting success was not addressed in this study, begging calls from nestlings may also be drowned out, leading to increased chick mortality. Finally, Villard, Martin & Drummond (1993) proposed that female passerines are more likely to settle in sites having a high male density. In a related experiment, detectability-adjusted point-count densities of singing male ovenbirds were greater at control sites than at compressor sites (Habib 2006). Lower densities of ovenbird males at compressor sites may reduce the probability that females will settle there.

While little work has been done on the specific issue of noise and bird pairing success, research comparing ovenbird pairing success in continuous vs. fragmented forests has found differences ranging from 10% to 50% (Villard, Martin & Drummond 1993; Van Horn, Gentry & Faaborg 1995; Bayne & Hobson 2001). The difference of 15% found in this study is at the low end of this range. However, whether differential pairing success influences population dynamics is unclear. Unmated males are common in many passerine species, which suggests that forest songbird populations naturally have inherent sex biases. If the mechanisms causing a differential sex bias in a population are driven by habitat-specific female survival or recruitment, then variable pairing success between high- and low-quality habitats

may be indicative of a negative demographic effect. Alternatively, females may simply be more reluctant to use one habitat over another. If all females in a population breed, and tend to do so in the best-quality habitats, then the effects of habitat-specific pairing success on population dynamics may be negligible.

The structure of vegetation in the territories of paired vs. unpaired birds played a role in determining male pairing success. We found that pairing success increased in areas having more complex territory structure. While Howell *et al.* (2000) found a negative association of ovenbird density with mean tree d.b.h., Van Horn & Donovan (1994) state that ovenbirds prefer habitats having large trees. This discrepancy probably comes from different definitions of what is meant by large trees, as studies in Missouri have found mean tree size is greater in territories of paired than unpaired males (Van Horn & Donovan 1994). Van Horn & Donovan (1994) emphasized the importance of litter depth in determining pairing success. Unreported models using litter depth as a measure of territory quality were not significant in our study. Habitat structure can influence the transmission of sound (Huisman & Attenborough 1991), so it is possible that birds with territories that have more habitat complexity are less impacted by noise because of greater attenuation. If this were the case, we expected the interaction between habitat structure and noise level to be significant. In unreported analyses, we found no evidence for this, but a limited sample size of unpaired males makes such effects difficult to detect.

At the individual level, we found no evidence that age or body morphology influenced pairing success. This is in contrast to previous work that has shown that older birds have greater pairing success than younger birds (Saether 1990; Bayne & Hobson 2001). A connection between age and pairing status in the presence of noise was found by Reijnen & Foppen (1994): within 200 m of a highway, young males willow warblers *Phylloscopus trochilus* were 25% less successful at attracting mates than older males, while farther from the road there were no differences in pairing success between age classes. This pattern could be explained by older birds being more experienced singers, which females may be attracted to despite the background noise.

AGE STRUCTURE OF POPULATION

Although we did not find an effect of individual age on pairing success, we did find that the age structure of ovenbirds near compressor sites was different from controls overall. How biased age structures form between habitats is not clear. Holmes, Marra & Sherry (1996) suggested that older black-throated blue warbler *Dendroica caerulescens* males occupy higher quality sites than younger males because older males outcompete younger birds for these areas. By claiming the highest quality territories early in the breeding season, older males may exclude younger males from good-quality habitats, thereby forcing younger males to use sub-

optimal sites. Our expectation was that this difference in age structure would explain the differences in pairing success we observed. That we did not find a direct relationship between age and pairing success at the individual level could be the result of the limited number of unpaired males available to test for age effects and/ or inaccuracies in ageing birds. Alternatively, females may use song characteristics to identify young or low-quality males and, in background noise, their ability to do so accurately is impaired. More work is required to test the generality of age-related variation in habitat selection in forest songbirds.

One prediction of ideal–despotic behaviour is that sites that are high quality will tend to be reoccupied in subsequent years by males that return to sites where they were previously successful (Bayne & Hobson 2002). We attempted to assess if young or unsuccessful breeders from 2004 would return to the same territory in 2005. This would have provided an indication of whether birds move away from noisy territories when settling the following year. In the first week of June 2005, we returned to all the locations where ovenbirds were captured in 2004. Using playbacks to attract the birds in the forested periphery of the cleared site where they had been caught the preceding year, we attempted to determine if there was a difference in return rate to the control vs. compressor sites. However, only one bird was resighted in 2005, at a compressor site. This low return rate is in distinct contrast to work by Porneluzi & Faaborg (1999), Burke & Nol (2001) and Bayne & Hobson (2002), who found that *c.* 40% of male ovenbirds return to the same territory from year to year in contiguous forest. One explanation for this extremely low return rate could be that ovenbirds at wellpads and compressor stations were universally affected by some other factor (e.g. high predation at edges) and subsequently never returned to either one of these anthropogenically disturbed areas. This phenomenon warrants further study.

If the pattern of age-related habitat selection were to manifest itself in females, the implications for ovenbird population dynamics could be more substantial. Young females attempting to breed for the first time often have lower reproductive output than older individuals having previous breeding experience (Holmes, Marra & Sherry 1996). In areas where young females are dominant, population sinks may form. Populations in sink habitats may only persist via immigration from other areas having less human disturbance (Robinson *et al.* 1995). Managers need to recognize that the presence of birds like the ovenbird near compressor sites and other industrial sites does not necessarily indicate that local populations are self-sustaining.

CONSERVATION IMPLICATIONS

As of September 2005, there are more than 5600 compressor stations in Alberta's boreal forest (IHS Energy, Calgary, Canada). However, there are also many other

types of noise-generating energy industry facilities, including gas plants, dehydration facilities and pump-jacks. Currently these disturbances exist in a region about three times the size of England. The proliferation of energy facilities is set to increase dramatically in this region over the next 5 years as a $100-billion influx of energy sector development is planned. The reduction in habitat amount as well as reduced breeding success in areas impacted by industrial noise could result in a large decrease in the amount of high-quality breeding habitat available for ovenbirds and other passerines. The effect may be particularly problematic in the eastern portion of Alberta, a region subject to extraction of bitumen by mining and steam-assisted gravity drainage (SAGD) procedures, which involve a substantial number of noise-generating facilities.

Compressor station clearings typically range from 1 to 4 ha in size. In the eastern portion of our study area, there are approximately 650 compressor station-type facilities. Assuming a conservative average cleared area of 2 ha pad^{-1}, this translates to 1300 ha of direct ovenbird habitat area lost to tree removal for compressor pads (including wellpads in this estimate would drastically increase the figure by more than 50 000 ha). If we assume that one ovenbird territory on each side of the perimeter of the compressor station pad has additional negative behavioural effects consistent with our findings, it results in an additional impacted area of nearly 13 000 ha. Adding 'impacted area' buffers around other noise-generating facilities would increase this figure considerably. Importantly, technology to decrease noise levels at industrial sites by *c.* 30 dB(A) does exist (ATCO Noise Management 2003). However, the financial costs to fit compressor stations with noise reduction technologies in wilderness areas has been deemed unnecessary because of the lack of impact on human residences (Alberta Energy & Utilities Board 1999). Our study demonstrates that noise *per se* does have an impact on breeding forest songbirds and that more careful assessment of noise effects is needed for future energy developments.

While previous studies looking at effects of roads on breeding birds (Reijnen & Foppen 1994; Reijnen *et al*. 1995; Reijnen, Foppen & Veenbaas 1997) have postulated noise as the cause of altered behavioural patterns, researchers have been unable to isolate it from confounding factors. This study provides the strongest support that chronic noise is an important factor influencing habitat quality. Our result supports the conclusions from road avoidance studies, which argue that noise is the key factor influencing birds in such environments. Consequently, adding busy roads to the list of noise-generating sites in Alberta and elsewhere in the world dramatically increases impacted area estimates.

Acknowledgements

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